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Potentiation of Odor Aversions Following Conditioning With Taste and Temperature

by

© Karen A. Stierhoff

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Dedication

To Larry -

past, present, and future

source of inspiration.

Abstract

Recent investigations have revealed that the toxiphobia conditioning of odors is potentiated when presented in simultaneous compound with taste during conditioning. Such findings are contrary to expectations derived from previous studies of compound conditioning which suggest that taste would compete with the conditioning of odor. Several mechanisms have been suggested for the potentiation findings, e.g., memorial indexing, based on taste categorizing odor as a food cue in memory, and within-compound conditioning, based on the summation of odor-US and taste-US associations via the odor-taste association. The present investigation examined implications of memorial indexing and within-compound conditioning accounts of odor potentiation under different combinations of stimuli which might be expected to affect the development of aversions to the particular components.

In the experiments, acquisition training consisted of two illness-inducing trials, one consisting of a conditioned stimulus presented separately and one consisting of a simultaneous stimulus compound. In Experiment 1, one odor was conditioned alone and a second odor was conditioned in compound with a taste stimulus. These conditions were repeated in Experiment 2, and with the addition of conditioning odor in compound with a temperature stimulus. This latter experiment also included a second phase, in which the aversions to the taste and temperature components

were extinguished. In Experiment 3, two temperature stimuli were conditioned alone and in compound with taste. In Experiment 4, odor, temperature, and taste were conditioned separately and together in a three-component compound. In all experiments, the consumption during exposure to target components was assessed in two non-reinforced "test" trials.

The principle findings were: (a) potentiated odor aversions following conditioning to odor-taste, odor-temperature, odor-taste-temperature compounds; (b) temperature was not potentiated when conditioned in compound with taste or with odor and taste; (c) taste was not potentiated when conditioned in compound with odor and temperature; (d) extinction of the taste or temperature associate of the odor attenuated the odor aversion.

The present findings extended the potentiation phenomenon, well documented with odor-taste compounds, to odor-temperature and odor-taste-temperature compound training procedures. Moreover, the attenuated odor aversion following extinction of the associate component suggests that an association between the components had been established during conditioning and that the association plays a critical role in manifesting odor potentiation. To encompass the observed pattern of potentiation as a stimulus-specific effect, it was suggested that the within-compound learning model be extended to include specific properties of the compounded stimuli as important factors in a potentiation effect.

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I. Introduction

When a solution with novel olfactory properties is given to thirsty rats and then followed by lithium-induced illness, rats later avoid these stimuli. Similarly, when a novel-colored solution is given to thirsty birds and followed by illness, the birds develop a color aversion. This phenomenon, often labelled "food-aversion learning," exhibits many parallels with Pavlovian conditioning (e.g., see Revusky, 1971), with the visual or olfactory cue corresponding to the conditioned stimulus (CS) and the illness corresponding to the unconditioned stimulus (US). Extensive research indicates that either modality, olfactory or visual, is a sufficient CS for avoidance responding (e.g., Taukulis, 1974; Wilcoxin, Dragoin, & Kral, 1971).

Recently, several investigators have demonstrated that odor (Durlach & Rescorla, 1980; Lorden, Kenfield, & Braun, 1970; Rusiniak, Hankins, Garcia, & Brett, 1979) or color (Brett, Hankins, & Garcia, 1976; Clark, Westbrook, & Irwin, 1979; Galef & Osborne, 1978; Lett, 1980) can acquire stronger aversive properties when simultaneously presented with a novel flavor and followed by lithium poisoning. For example, if rats receive odor in compound with taste prior to toxicosis, the subsequent avoidance of that odor is greater relative to when odor is conditioned by itself. The presence of taste can be said to "potentiate" the conditioning of the odor.

Potentiation can be contrasted with the Pavlovian phenomenon of overshadowing. In cases of overshadowing, a target CS presented in compound with a second CS during conditioning elicits a conditioned response of lesser magnitude than would be observed had the target CS been conditioned by itself. The second stimulus is said to "overshadow" the conditioning of the target CS (Pavlov, 1927).

Overshadowing has been demonstrated in a variety of conditioning preparations such as instrumental discrimination learning (e.g., D'Amato & Fazzaro, 1966; Miles & Jenkins, 1973), conditioned suppression (e.g., Kamin, 1969; MacKintosh, 1971), conditioned reinforcement (e.g., Egger & Miller, 1962, 1963), and food-aversion learning (e.g., Revusky, 1971). Consequently, most current models of compound-cue conditioning (e.g., MacKintosh, 1975; Rescorla & Wagner, 1972; Sutherland & MacKintosh, 1971) include an interpretation of overshadowing phenomena. These models generally suggest that elements of a reinforced compound compete with one another for conditioning by a consequent US. Such competition might be expected to attenuate, rather than potentiate, conditioning of an aversion to odor or color when presented in compound with taste. The fact that potentiation can occur challenges these general models of conditioning.

A variety of explanations have been offered to account for the potentiation effect. Garcia and his co-workers

(Garcia & Rusiniak, 1980; Palmerino, Rusiniak, and Garcia, 1980; Rusiniak et al., 1979) have suggested a "memorial indexing" account of potentiation in which the functional and structural differences between the olfactory and gustatory systems are emphasized. These investigators have noted that the rat uses olfaction as a multipurpose information channel to guide appetitive approach to food sources, avoid predators, and select mates. Thus the animal is likely to encounter many significant odors between the odor of a poisoned meal and the onset of toxicosis. These intervening odors might be expected to interfere with learning about the food-related odor. In contrast, tastes are primarily involved in consumption and therefore less susceptible than odor to interfering stimuli not related to ingestion. According to the memorial indexing hypothesis, when odor and taste are part of a poisoned meal, "...the taste of the meal [becomes] a critical index for the specific odor that must be retrieved from memory to avoid poison" (Rusiniak et al., 1979, p.15). Likewise, "other odors do not interfere, because each odor is indexed to its own respective behavioral system" (Garcia & Rusiniak, 1980, p.152).

Proponents of the memorial indexing interpretation of potentiation cite anatomical evidence in support of the theory. Gustatory fibers are known to project to the same brain stem area that receives visceral fibers controlling emesis. Olfactory fibers project to the limbic system in the

forebrain and do not have direct access to the brain stem emetic system. When odor and taste are presented simultaneously, a postulated "and-gate" mechanism controlled by taste allows information about the odor access to the emetic memory system (Palmerino et al., 1980). As a result, odor is able to form a stronger association with illness than if it had been conditioned alone.

An alternative view of the potentiation effect has been offered by Durlach and Rescorla (1980). They suggest that the phenomenon occurs because of an association established between odor and taste, i.e., a "within-compound" association (see Rescorla & Cunningham, 1978), as a result of the co-occurrence of these stimuli during conditioning. According to this hypothesis, three different associations are formed during the simultaneous pairing of an odor and taste with illness: an association of odor with illness, an association of taste with illness, and an association of odor with taste. Presenting the odor stimulus during testing is assumed to activate not only the odor-illness association but the odor-taste association as well. The odor-taste association in turn activates the taste-illness association. Thus the potentiated odor aversion occurs not because odor has a stronger association with the illness US but because odor has an additional association with a taste that is also aversive (Rescorla and Durlach, 1981).

The present research sought to discriminate between the memorial indexing and within-compound association accounts

of potentiation through an examination of several different predictions based on each account. The following comparison of these differential predictions suggests several relevant empirical bases to begin that search.

One noted difference (Lett, 1983; Rescorla & Durlach, 1981) between the two interpretations of potentiation is in the roles assigned to the taste aversion. According to the memorial indexing hypothesis, taste acts as a catalyst to increase the strength of the odor-illness association during the poisoning process. This has been interpreted as suggesting that the strength of the potentiated odor aversion is independent of the current aversiveness of the taste. If so, changing the value of the taste before testing should not affect the potentiated aversion to odor. On the other hand, if potentiation depends upon the summation of the odor-illness and taste-illness associations caused by the within-compound odor-taste association, the current strength of the taste aversion would be critical. Weakening the taste-illness association during the interval between conditioning and testing means that responding to the odor would no longer involve two sources of aversion and potentiation would be disrupted.

Several similar experiments have examined these differential predictions, but have provided conflicting results (Durlach & Rescorla, 1980; Lett, 1983; Palmerino, 1979, cited in Lett, 1983). In each experiment, compound odor-taste conditoning was followed by repeated

non-reinforced exposures to the taste stimulus so as to extinguish taste's aversiveness. Lett (1983) and Palmerino (1979, cited in Lett, 1983) found marked odor aversions both in animals with extinguished taste aversions and in animals given no taste extinction treatment. Both groups drank significantly less unflavored water in the presence of the odor cue that had been conditioned with taste than animals conditioned to the same odor without taste. Consistent with the memorial indexing hypothesis, these results suggest that odor potentiation does not depend upon an underlying taste aversion. In contrast, Durlach and Rescorla (1980) found that after the taste extinction phase, the aversion to the odor previously paired with the taste was no different than the aversion to an odor conditioned by itself, and was significantly smaller than the aversion to an odor paired with a non-extinguished taste. In this case, then, extinction of the taste aversion seemed to disrupt the potentiated odor aversion, which suggests that continued aversion to the taste is necessary to obtain potentiation in the manner anticipated by an account in terms of within-compound associations.

Lett (1983) has suggested that this discrepancy in findings occurred as a result of procedural differences between the studies. Durlach and Rescorla (1980) administered one (Experiment 3) and two (Experiment 4) non-reinforced presentations of the odor-taste compound prior to pairing the compound with poisoning. Neither Lett

(1983) nor Palmerino (1979, cited in Lett, 1983) provided any preconditioning exposures to the odor-taste compound before pairing it with poison. As Durlach and Rescorla suggest, extinction of the taste component in isolation seems to have disrupted the odor-taste association in their experiments. However, the odor-taste association may have been formed during the preconditioning exposure period rather than during the conditioning trial. If so, Durlach and Rescorla may have demonstrated only that within-compound associations occur, not that these associations are the sole basis of potentiation. The findings of Palmerino and Lett indicate that when the stimuli are not pre-exposed, odor potentiation is not adversely affected by extinction of the taste aversion. Therefore one might conclude, in accordance with Lett, that the taste and potentiated odor aversions at the time of test are independent as predicted by the memorial indexing account.

If Lett's conclusion "...that within-compound learning is not responsible for the [odor] potentiation effect" (Lett, 1983, p.24) is accepted, the problem remains of how to account for the absence of odor potentiation following taste extinction in the experiments of Durlach and Rescorla (1980). That is, if pre-exposing the odor-taste compound does establish a within-compound association between odor and taste, and if disrupting that association by later extinguishing the taste aversion disrupts the potentiation of odor, then it seems that within-compound learning does

play some role in the effect. Moreover, the memorial indexing hypothesis offers no suggestion as to why pre-exposing the odor-taste compound should have any effect, either facilitative or disruptive, on odor potentiation.

A second difference between the two accounts of potentiation concerns the necessity of taste as a component during conditioning. According to the memorial indexing account, taste plays a requisite role in producing odor potentiation by endowing odor with some of the properties of taste (Palmerino et al., 1980). Odor, thus categorized as a food cue, is able to form a stronger aversion with the illness US. On this view, it would be predicted that without the facilitating presence of taste during conditioning, odor would not acquire potentiated aversive properties. Interestingly, taste has been a conditioned component in virtually all of the reports of potentiation within food-aversion learning situations.

The within-compound association account of potentiation does not explicitly require that taste be one of the components of the compound. The enhanced conditioned response is thought to depend upon the conditioned association between the two elements which summates with each element's association with the US (Durlach & Rescorla, 1980). Accordingly, potentiated conditioning should not only occur following odor-taste conditioning, but following simultaneous conditioning of any stimuli that can form within-compound associations. If the taste stimulus, via the

within-compound odor-taste association, simply provides an additional source of aversion, one might expect that conditioning odor with any other stimulus would produce a potentiated odor aversion. It also seems plausible, according to the within-compound association account, that the presence of taste could potentiate the conditioning of an accompanying stimulus other than odor.

Comparison of the memorial indexing and within-compound association accounts of potentiation has illustrated several unanswered questions concerning theories of how and why potentiation can occur. First, what is the role of within-compound learning between the odor and taste stimuli without preconditioning stimulus exposure? The memorial indexing account suggests no critical role for a conditioned association between odor and taste in producing potentiation, whereas the within-compound association account assumes an odor-taste association is the basis of the effect. Second, is potentiation unique to compounds containing taste, odor, or both? According to the memorial indexing account, potentiation is limited to compounded tastes and odors by virtue of their respective structural and functional systems. Conversely, no specific stimuli or stimulus characteristics are suggested in the within-compound association account.

The present series of experiments addresses these questions. The potentiation of odor stimuli was examined, and it is proposed that the findings may be generalizable to

color potentiation. The first experiment provided a well-controlled demonstration of potentiated odor conditioning following compound conditioning with taste. The second and third experiments investigated the necessity and sufficiency of taste as a compound component in a potentiation outcome. Because theories concerning the underlying mechanism of potentiation assign different levels of importance to taste in producing the effect, the results would provide direct evidence for determining the neccessity of certain stimuli in enhancing conditioned responding to paired associates. The second experiment was also designed to examine whether a within-compound association between simultaneously conditioned stimuli contributes importantly to potentiated responding in the absence of preconditioning stimulus exposures. The fourth experiment examined whether the potentiation effect can be extended to learning situations involving a three-component compound.

II. Experiment 1

Several different methods of odor stimulus delivery have been employed in studies of potentiation. Some investigators have obtained odor potentiation by adding the odorant directly to the drinking water that contains a novel flavor (Rusiniak et al., 1979; Durlach & Rescorla, 1980). Although special tests have suggested otherwise (Rusiniak et al., 1979), this method of odor presentation appears somewhat problematic because the odorant may impart taste as well as odor properties. Other investigators have presented the odor and taste stimuli via separate media so the odorant was less likely to be tasted (e.g., Lett, 1983; Palmerino et al., 1980). In accordance with the logic of the latter method, the system employed here involved delivering the odor through a ventilation system as animals were given an opportunity to drink specific solutions.

The design of the present experiment was similar to that used by Durlach and Rescorla (1980, Experiment 5). Rats were each poisoned following exposure to two different odor stimuli: an odor presented alone (A) and another odor (B) presented in compound with a taste (X). After conditioning, aversions were assessed by comparing distilled water consumption during separate presentations of the A and B odor stimuli. The question of interest was whether drinking would be less during exposure to B, the odor conditioned in compound with taste, than during A, the odor conditioned alone. Less consumption in the presence of B would

demonstrate a potentiation effect due to compound conditioning with taste.

Method

Subjects. The subjects were 16 male Holtzman rats about 90 days old at the start of the experiment. They were housed in individual Wahmann wire-mesh cages.

Apparatus. All experimental treatments took place in four identical conditioning chambers located in a room separate from the colony room. An experimental chamber consisted of a clear acrylic plastic box (30 cm x 13 cm x 11.5 cm) sealed at all seams to make it as airtight as possible. The front panel had an "odor tunnel" (7.5 cm x 6.5 cm x 6 cm) which protruded outward and which opened into the experimental chamber. At the top center of this odor tunnel a 1.7 cm hole was drilled to accommodate the water spout of an inverted 250 ml bottle. At the back of this tunnel, filter paper was affixed for delivery of the odor stimulus. A 12 cm exhaust fan situated on the rear panel of the experimental chamber drew air out through the filter paper, odor tunnel, and chamber and into 10.2 cm plastic tubing through which air was carried to the building's ventilation system. This fan was in operation continuously throughout all experimental sessions.

The odorants were a 2% (v/v) solution of Empress brand almond extract (ALM - almond odor) and a 2% (v/v) solution of ethyl butrate (PINE - pineapple odor). The odors were

presented by placing 1 ml of the solution on the filter paper just prior to placing the animal into the chamber. This amount of odor solution was sufficient to maintain saturation for a 5-min stimulus exposure period. The taste stimulus was a 2% (w/v) solution of sucrose (SUC). All stimuli were dissolved in distilled water. The odor-taste compound was created by placing the odorant solution on the filter paper and sucrose in the drinking bottle. When only the odor cue was presented, the drinking bottles contained distilled water at room temperature (25°C).

Procedure. All animals were adapted to a water deprivation schedule that permitted access to room-temperature distilled water for a period of 15 min each day. Then for a 7-day period, they were habituated to drinking distilled water for 5 min in the conditioning chamber. During each habituation session and throughout the experiment, amount consumed was measured by weighing the bottles before and after each 5-min drinking period. Approximately 1 hr later, the rats were given access to water for 15 min in the home cages. This was to ensure that all rats received an adequate supply of water. Food was removed prior to each habituation and training session and replaced after the water access in the home cages to avoid any adventitious pairing of food tastes with the toxin or with the flavor CS.

On Day 1 of the experiment, half the animals received a 5-min exposure to an odor by itself (A) in the conditioning

chamber and half received similar exposure to an odor-taste compound stimulus (BX); on Day 3, each received the other stimulus. Half of the animals received ALM as A and PINE as B; the other half received PINE as A and ALM as B. The taste, X, was sucrose (SUC) for all animals. Following each exposure to the A and BX stimuli, animals received a 5 ml/kg ip injection of 0.6 M lithium chloride (LiCl). Then they were returned to their home cages in the colony room. Days 2 and 4 were recovery days during which animals received 5-min access to distilled water in the conditioning chamber.

Testing was conducted on Days 5 and 6. On Day 5 half the animals (four animals conditioned to ALM alone and four animals conditioned to PINE alone) were given a 5-min exposure to ALM while drinking water. The remaining half of the animals were given similar exposure to PINE. On Day 6 each animal received the other odor stimulus.

Results

Training data. The average consumption on the habituation day just prior to the first conditioning day was 10.3 gm. The mean levels of consumption (collapsed across the two conditioning days) were 10.0 gm, 10.3 gm, 10.4 gm, and 10.7 gm for ALM, PINE, ALM-SUC, and PINE-SUC, respectively. The data of the training consumption levels were analyzed using analysis of variance (ANOVA) with one between-subjects factor, paired odor (ALM vs. PINE), and one within-subjects factor, treatment (A vs. B). There were no

significant main effects and no interaction, *F*s <1. This indicates that consumption of any one solution during training did not differ reliably from any of the others. In addition, poisoning on the first conditioning day did not disrupt consumption on the second conditioning day. Mean consumptions on the first and second conditioning days (collapsed over solutions) were 10.2 gm and 9.9 gm, respectively. This suggests that there was relatively little generalization between the odor conditioned alone and the odor conditioned with taste.

Test data. During testing, animals were given separate exposures to the A and B odor stimuli. Figure 1 (see Appendix 2) shows a comparison of the mean water consumption during presentations of these stimuli over the two days of testing, separated according to whether each was ALM or PINE. The data were analyzed using ANOVA with one between-subjects factor, paired odor (ALM vs. PINE), and one within-subjects factor, treatment (A vs. B). An odor potentiation effect was indicated by a significant main effect of treatment, $F(1,14)=26.81$, $p<.001$. Animals tended to drink less water during the presentation of B, which had been conditioned in compound with taste, than during A, which had been conditioned alone. There was no main effect of paired odor, $F(1,14)=4.13$, $p>.05$, which indicates no overall difference in the consumption of either ALM or PINE. The interaction between treatment and paired odor was not significant, $F(1,14)=3.40$, $p>.05$.

Discussion

The lower level of consumption during exposure to B relative to A demonstrated that an aversion to odor can be potentiated by the presence of taste during conditioning. An odor simultaneously conditioned with taste can acquire stronger aversive properties than an odor conditioned by itself. Thus potentiation of odor with taste is replicable in our laboratory using procedures in which the odor and taste stimuli are explicitly separated during presentation. Such replication is important because some investigators have been unable to produce odor potentiation with taste (Bouton & Whiting, 1982; Mikulka, Pitts, & Philput, 1982). Unfortunately, the exact conditions under which potentiation does or does not occur have yet to be determined.

It should be noted that an effect similar to potentiation has also been observed in several preparations designed to study serial compound conditioning. These include the conditioned nictitating response (Gormezano and Kehoe, 1983), autoshaping (Kaplan and Hearst, 1983; Rescorla, 1982), and conditioned fear using a shock US (Pearce, Nicholas, and Dickinson, 1981). In serial conditioning, two stimuli are presented successively and followed later by a reinforcer. In each of the studies demonstrating a potentiation effect, the conditioned response to a target CS was enhanced when it had been followed by a second CS before reinforcement, relative to trace conditioning of the target CS. Although various

theories are offered to explain the occurrence of potentiation with serial compounds, each is quite different from those suggested for simultaneous compound potentiation and neither the serial conditioning potentiation theories nor the simultaneous conditioning potentiation theories captures both patterns of results. Indeed, conditioning of the two types of compounds may not be directly comparable (Rescorla, 1980), and any potentiation effect observed with simultaneous or successive compounds may not involve similar mechanisms.

III. Experiment 2

Experiment 1 demonstrated a reliable potentiation effect under conditions that separated the sources of odor and taste. As discussed previously, there have been two major theoretical accounts concerning how potentiation occurs. The memorial indexing and within-compound association accounts of potentiation both suggest that the effect may depend upon a special interaction between the components of the compound stimulus. The accounts differ, however, regarding the components that are designated as essential for potentiation. The memorial indexing account, which assumes that taste operates to increase the association between odor and the illness US, would predict that odor potentiation would not occur if taste was not an element of the conditioned compound. In contrast, according to the within-compound association account, odor potentiation depends upon the conditioned association between the compound elements; the account offers no assumptions about what those elements should be. On this view, odor potentiation could occur when odor and taste are conditioned together, as well as when odor and, for example, a distinctive temperature cue (the drinking solution heated or cooled) are conditioned together. Temperature may be a sufficient CS in establishing odor potentiation because temperature, like taste, can also acquire aversive properties when paired with illness (Nachman, 1970).

The present experiment was conducted to determine if the presence of a taste stimulus is a necessary condition for the potentiation effect. Rats were given the A,BX treatment of Experiment 1, but the procedure differed with respect to the nature of the X cue. For half the animals, X was a taste cue; for the other half, X was a specific temperature cue. If an account in terms of memorial indexing is correct, this procedure should result in the potentiated rejection of the odor paired with taste but not the odor paired with temperature. Alternatively, the within-compound association account would predict that odor potentiation would occur following both odor-taste and odor-temperature conditioning as long as an association had been formed between the compounded elements.

The present experiment included a second conditioning phase in order to determine if such a within-compound association had indeed been established between the elements of the compound. During this latter phase, half of the animals were given repeated non-reinforced presentations of X (taste or temperature) to extinguish the aversion to X. During testing, animals received separate exposures to A and B. Based on previous findings (Lett, 1983; Palmerino, cited in Lett, 1983), extinction of the taste and/or temperature aversions should not affect the potentiated odor aversion, at least in part because the stimuli were not pre-exposed. On the other hand, if extinction of the taste and/or temperature aversion does disrupt the odor potentiation,

i.e., a similar level of aversion between the odor whose X partner was extinguished and the odor conditioned alone, then this would be evidence that a within-compound association between conditioned components can occur without preconditioning stimulus exposure trials. More importantly, a disruption of odor potentiation would demonstrate that the within-compound association contributes to the potentiated aversion exhibited to odor.

Method

Subjects. The subjects were 64 male Holtzman rats about 90 days old at the start of the experiment. All animals were housed in individual wire-mesh cages.

Apparatus. The apparatus was identical to that used in Experiment 1. The taste (SUC - sucrose), odor (ALM - almond; PINE - pineapple), and odor-taste stimuli used were also identical to those of the previous experiment. The temperature stimulus (HOT - hot) was the drinking solution heated to 40°C. The odor-hot compound was created by placing 1 ml of the odor solution on the filter paper and using distilled water at 40°C in the drinking bottles.

Procedure. All animals were adapted to a water deprivation schedule that permitted access to room-temperature distilled water for a period of 15 min each day. Then for a 5-day period they were habituated to drinking for 5 min in the conditioning chamber located in a separate room. The animals received access to food and

drinking water in the same manner as in Experiment 1.

The design of this experiment is outlined in Table 1 (see Appendix 1). The animals were divided into four equal groups. Each animal received an odor-alone solution (A). In addition, two groups, Group TaExt and Group TaNo, received SUC as X in compound with odor (B). The remaining two groups, Group TeExt and Group TeNo, received HOT as X in compound with B. For purposes of counterbalancing, half the animals in each group received ALM as A and PINE as B, while the remaining half received PINE as A and ALM as B. On the first day, half the animals in each group were given exposure to A; the other half were given exposure to BX. On the third day, the alternate solution was presented to each animal. Immediately following each presentation of the experimental solutions, all animals received a 5 ml/kg ip injection of .6 M LiCl. On the intervening day (Day 2), animals were given access for 5 min to distilled water at room temperature in the experimental chambers.

A second conditioning sequence was administered over the next 5 days. During this time, Groups TaExt and TeExt were given non-reinforced presentations of X. On each day these animals received 5-min access to SUC or HOT in the conditioning chambers. Groups TaNo and TeNo received a daily 5-min access to water at room-temperature in the conditioning chambers.

Testing was conducted over the next two days. Each animal was presented with separate exposures to ALM and PINE

for a period of 5 min each day in the same manner as tests in the previous experiment.

Results

Training data. During the conditioning periods, there was no significant difference among the consumption levels of the particular solutions, *F*s <1. Mean consumption of the six different solutions fell within a range from 6.2 gm (PINE-SUC) to 8.1 gm (PINE-HOT). As in the previous experiment, poisoning on the first day of conditioning did not disrupt consumption on the second conditioning day. Mean amounts of fluid consumed on the first and second days (collapsed over solutions) were 8.3 gm and 7.6 gm, respectively.

On the first day of extinction, mean consumption was 1.1 gm of SUC and 2.3 gm of HOT. These low levels indicated that aversion had developed to SUC and HOT. Consumption of both solutions rose over the course of extinction such that on the fifth and final day the mean levels of consumption were 6.7 gm and 7.8 gm of SUC and HOT, respectively.

Test data. The test data were analyzed using ANOVA with three between-subjects factors - modality (taste vs. temperature), extinction training (extinction vs. no extinction), and paired odor (ALM vs. PINE); and one within-subjects factor, treatment (A vs. B). The mean consumption of A and B during testing is presented in Figure 2 (see Appendix 2). The left portion of the figure displays

the average consumption for Groups TaNo and TeNo; the right portion displays the average consumption for Groups TaExt and TeExt.

One important question in the present experiment concerned whether odor potentiation can occur when odor is conditioned with temperature as well as with taste. This issue can be addressed by analyzing the Modality x Treatment interaction within the groups given no extinction training (Groups TaNo and TeNo). The results indicated a nonsignificant interaction, F (1,30)<1. Individual comparisons revealed that reliably less consumption occurred during test exposure to B relative to A for Group TaNo, $t(15)=3.76$, $p<.01$. This indicates an odor potentiation effect following odor-taste conditioning. In addition, the consumption during exposure to B relative to A for Group TeNo was significantly less, $t(15)=3.22$, $p<.01$, which indicates that temperature conditioned in compound with odor also resulted in an odor potentiation effect.

The Extinction training x Treatment interaction addresses a second important question regarding whether extinction of the X cue following compound conditioning has any effect on the subsequent consumption of the odor that had been paired with X. The results indicate a significant interaction effect, F (1,56)=27.26, $p<.001$. Individual comparisons revealed that Groups TaNo and TeNo tended to drink less during exposure to B than during A, t (31)=4.98, $p<.01$, while Groups TaExt and TeExt demonstrated no

differential consumption of A and B, $t(31)=.76$, $p>.10$. This implies that X extinction served to eliminate the odor potentiation effect.

The main effect of modality was not significant, $F(1,56)= .08$, $p>.10$, which indicates that animals showed no overall differential consumption when conditioned with SUC as a compound element versus HOT as a compound element. In addition, modality did not interact reliably with either paired odor or treatment, $Fs(1,56)<2.65$, $ps>.10$. The Modality x Extinction training interaction was significant, $F(1,56)=5.38$, $p<.05$. This may suggest that extinction of the taste aversion had a stronger disruptive effect on the odor aversion than extinction of the temperature aversion. Modality x Paired odor x Treatment interaction, $F(1,56)=8.96$, $p<.01$, and the Modality x Extinction training x Treatment interaction, $F\ (1,56)=2.90$, $p<.01$, were significant.

Animals showed no overall difference in intake of ALM or PINE, $F(1,56)= 1.79$, $p>.10$, and this factor did not interact significantly with any of the other factors, $Fs(1,56)<2.65$, $ps>.10$.

Discussion

The pattern of results observed in this experiment replicates the previous findings of potentiated odor aversion learning when odor and taste are conditioned together. Animals in the present experiment that were not

given sucrose extinction trials (Group TaNo) received essentially the same A,BX treatment as the animals in Experiment 1. During testing, both sets of animals drank less water during exposure to B than during exposure to A.

More importantly, the results also suggest that temperature conditioned in compound with odor can potentiate the subsequent aversion to odor. Group TeNo, trained with X as HOT and no subsequent HOT extinction trials, tended to drink less during test exposure to B than during exposure to A. Odor potentiation following odor-temperature conditioning is at odds with the memorial indexing hypothesis that potentiation is due in part to the presence of taste during conditioning. However, if the assumption that taste is a necessary component for potentiation is broadened to stimuli perceived by the tongue, then both temperature and taste could produce a potentiating effect on an accompanying odor. An interpretation of temperature as a tongue sensation allows enhanced odor aversion following odor-temperature conditioning to be explained in terms of memorial indexing.

In the within-compound account, odor potentiation is not limited to odor-taste compounds. Therefore, odor potentiation following odor-temperature conditioning could be explained using the same within-compound mechanism as applied to odor-taste conditioning. An assessment of whether within-compound learning indeed contributes to potentiation comes from comparing the results of animals given X extinction trials and those given no extinction trials. A

comparison of the mean intakes during A and B stimulus exposures for Groups TaNo and TeNo indicates that aversions to B, the odor conditioned with SUC or HOT, were potentiated. However, Groups TaExt and TeExt showed no differential consumption during test presentations of A and B. The overall difference in consumption of the extinction and no-extinction groups illustrates that changing the value of the taste component or temperature component of the conditioned compound disrupted the manifestation of the potentiated aversion to odor. This is direct evidence that a within-compound association can be established between the elements of a compound and that the association contributes substantially if not entirely to the potentiation effect. In addition, the potentiation effect was demonstrated in the absence of preconditioning exposure, a unique finding that is discrepant with previous reports (Lett, 1983; Palmerino, cited in Lett, 1983).

One aspect of the present procedures differs from that of Lett (1983) and Palmerino (cited in Lett, 1983) and may account for the separate findings. A typical experiment of Lett or Palmerino involved two odor-taste compound conditioning trials. In the present experiment, only one compound conditioning trial was given. Although multiple conditioning trials are not necessary for potentiation (e.g., Durlach & Rescorla, 1980; Rusiniak et al., 1979), increased compound presentations may operate to increase the associative strength of the CS-US associations (e.g.,

Rescorla & Wagner, 1972), thereby requiring more extinction trials to devalue the conditioned response to one of the components. Lett and Palmerino may have eliminated odor potentiation had more taste extinction trials been presented.

IV. Experiment 3

The results of the previous experiment indicated: a) potentiation of odor aversion learning can occur following conditioning of both odor-taste and odor-temperature compounds, and b) a within-compound association conditioned between the components plays a critical role in that potentiation. If the important factor in potentiation is an association established between the elements of the conditioned compound, then the effect may occur with compounds outside those containing odor. That is, potentiation may not depend upon the characteristics of the particular elements involved.

The question addressed by the present experiment is whether temperature is potentiated when conditioned with taste, i.e., whether the presence of a novel taste cue during aversive compound conditioning with a novel temperature cue results in an increase in the strength of the temperature aversion. To examine this possibility, rats were given the A,BX treatment of previous experiments, but A and B were now temperature cues while X was a taste cue. Following the conditioning of the two solutions, animals were given separate exposures to A and B. To the degree that taste potentiates a temperature aversion, B should be rejected relative to A.

Experiment 3A

Method

Subjects. The subjects were 16 male Holtzman rats approximately 90 days old at the start of the experiment. Each was housed in a separate hanging wire-mesh cage.

Apparatus. The apparatus was identical to that used in the previous experiments.

The temperature stimuli used were 40°*C* (HOT) and 10°*C* (COLD). The taste stimulus was a 2% (w/v) solution of sucrose (SUC) dissolved in distilled water. The two temperature-taste compounds were created by heating or cooling the sucrose solution to 40°*C* or 10°*C*, respectively.

Procedure. All animals were adapted to a water deprivation schedule that permitted access to distilled water at room-temperature (25°*C*) for a period of 15 min each day. During adaptation and throughout the experiment, food was removed just prior to fluid access and returned approximately 1 hr later. For the 5 days following adaptation, all animals were habituated to drinking for 5 min in the conditioning chamber located in a separate room.

Conditioning was carried out over the first three days of the experiment. Each animal received a temperature solution (A) and a temperature-taste solution (BX). On the first day, half the animals received access to A and half received access to BX; on the third day each received the other stimulus. Half the animals received COLD as A and HOT as B; the remaining animals received HOT as A and COLD as B. The taste X was SUC for all animals. Immediately following each 5-min exposure to the experimental solutions, animals

received a 5 ml/kg ip injection of .6 M LiCl. Then they were returned to their home cages in the colony room. During training and testing, 15-min access to distilled water at room-temperature was given in the home cages approximately 1 hr following the delivery of the experimental solutions. Days 2 and 4 were recovery days during which all animals received 5 min access to room-temperature distilled water in the conditioning chambers.

Testing was conducted on Days 5 and 6. On Day 5 half the animals in each group were given a 5-min exposure to the HOT solution and half the animals were given similar exposure to the COLD solution. On Day 6 each animal received the other stimulus.

Results

Training data. During the conditioning periods, there was little difference among the consumptions of the particular solutions, *F*s <1. Mean amounts consumed of the four different solutions were 9.3 gm, 10.0 gm, 10.7 gm, and 11.1 gm for COLD, COLD-SUC, HOT-SUC, and HOT, respectively. Conditioning on the first day did not disrupt consumption on the second conditioning day. Mean intakes (collapsed over solutions) on the first day was 9.9 gm and on the second day was 11.0 gm.

Test data. During the test periods, animals were given separate 5-min exposures to COLD and HOT. Figure 3 (see Appendix 2) compares the consumptions of A and B over the

two days of testing. Of primary importance is whether consumption of either temperature cue is affected by the presence of taste during conditioning. The data were subject to ANOVA with one between-subjects factor, paired temperature (COLD vs. HOT), and one within-subjects factor, treatment (A vs. B). The analysis revealed nonsignificant main effects of paired temperature and treatment, both Fs(1,14)<1. The interaction was also not significant $F(1,14)=2.05$, $p>.10$.

Discussion

The results of this experiment provide little evidence of the potentiation effect demonstrated in previous experiments. When a novel temperature cue is conditioned in compound with taste, the strength of the aversion to the temperature is not enhanced. The pattern of findings thus far has been that while the presence of taste or temperature in compound with odor can potentiate odor conditioning, taste does not enhance conditioning to temperature.

However, there is at least one factor in the present experiment that makes the absence of temperature potentiation somewhat equivocal. The lack of a detectable difference in consumption during presentation of the two temperature cues may be because rats were unable to discriminate between the two temperatures. Thus, Experiment 3B was conducted to replicate Experiment 3A and to determine whether novel temperature cues can acquire aversions.

Experiment 3B

Method

Subjects. The subjects were 32 male Holtzman rats. Each was approximately 90 days old at the start of the experiment. All animals were housed in individual cages.

Apparatus. The apparatus and experimental stimuli were identical to that used in Experiment 3A.

Procedure. All subjects were adapted to a water deprivation schedule that permitted access to distilled water at room temperature for a period of 15 min each day. During adaptation and throughout the experiment, food was removed just prior to fluid access and returned approximately 1 hr later. For the 5 days following adaptation, all animals were habituated to drinking for 5 min in the conditioning chambers located in a separate room.

The subjects were assigned to two equal groups. Conditioning was carried out over the first three days of the experiment. One group of animals, Group TeS, received access to a temperature solution (A) and a temperature-taste solution (BX). On Day 1, half the animals in this group received COLD as A and half received HOT as B; the other half received HOT as A and COLD as B. The taste X was SUC for all animals. On the third day each received exposure to the other solution. Immediately following each 5 min exposure to the experimental solution, each animal was given a 5 ml/kg ip injection of .6 M LiCl.

In the remaining group, Group Te, each animal received access to two temperature solutions only. On Day 1, half the animals were given a 5 min presentation of COLD and half were given a similar presentation of HOT. On the third day each received the other solution. Half the animals received a .6 M LiCl (5 ml/Kg) ip injection following exposure to COLD and half received a similar injection following HOT presentation.

Following the injections all animals were returned to their home cages in the colony room. During training and testing, animals received 15-min access to distilled water at room temperature in the home cages approximately 1 hr following the delivery of the experimental solutions. Days 2 and 4 were recovery days during which all animals received 5-min access to room-temperature distilled water in the conditioning chambers.

Testing was conducted on Days 5 and 6. On Day 5 half the animals in each group were given 5-min exposure to HOT and half were given similar exposure to COLD. On Day 6 each animal received the other solution.

Results

Training data. During the conditioning periods, mean consumption of the four different solutions, collapsed over the two days, was 7.5 gm, 8.1 gm, 9.0 gm, and 9.3 gm for COLD-SUC, HOT-SUC, COLD, HOT, respectively. There was no difference in average consumption levels of these solutions,

*F*s <1. Poisoning on the first conditioning day did not adversely affect consumption on the second conditioning day. Average amounts of solution drunk on both conditioning days (collapsed over stimuli) were 8.92 gm and 8.94 gm, respectively.

Test data. The mean consumption of the target solutions during testing is presented in Figure 4 (see Appendix 2). The data of Group Te were subject to ANOVA with one between-subjects factor, poisoned temperature (HOT vs. COLD), and one within-subjects factor, treatment (poisoned vs. non-poisoned). The main effect of posioned temperature was significant, $F(1,14)=4.62$, $p<.05$. Animals tended to drink less HOT than COLD. The main effect of treatment was significant, $F(1,14)=43.72$, $p<.001$, which indicates that the poisoned temperature was consumed less relative to the temperature that had not been poisoned. The Poisoned Temperature x Treatment interaction was not significant, $F(1,14)<1$.

The data of Group TeS were similarly analyzed with paired temperature (HOT vs. COLD) as a between-subjects factor and treatment (A vs. B) as a within-subjects factor. The analysis revealed nonsignificant main effects of paired temperature and treatment, both Fs$(1,14)<1$. The interaction was also not significant, $F(1,14)=1.75$, $p>.10$. This indicates that there was no differential consumption of either type of temperature cue regardless of whether it had been presented alone or in compound.

Finally, the two groups were compared for their overall consumption of HOT and COLD cues. The data were subject to ANOVA with two between-subjects factors, poisoned temperature (HOT vs. COLD) and group (Group Te vs. Group TeS). The analysis revealed no significant effects, *F*s <1, *p*s>.10.

Discussion

A consistent pattern of results was obtained between this experiment and Experiment 3A. In both cases a taste in simultaneous compound with a novel temperature during conditioning appeared to have no effect on the strength of the aversion to that temperature. Animals drank equivalent amounts of the temperature conditioned alone and the temperature conditioned with taste. These results cannot be attributed to an inability to discriminate between the two temperature stimuli because animals given discrimination training with poisoned and non-poisoned temperature cues developed reliable aversions to the poisoned temperature only.

The present findings could be interpreted in terms of the memorial indexing account, which confines occurrences of potentiation to odor-taste conditioning. Temperature afferents, presummably by virtue of their structure or brain projection site, would not be processed in memory with taste afferents in the same manner as odor and taste afferents.

The absence of enhanced temperature conditioning is not consistent with the within-compound association hypothesis, which offers no limitations on the type of stimuli that can develop potentiated CRs. According to this account, temperature conditioned in compound with taste should result in potentiation in the same manner that odor conditioned in compound with taste results in potentiation.

V. Experiment 4

The results of the previous experiments have indicated that learning about the odor element of a reinforced compound can be increased when the accompanying element is either taste or temperature, but that learning about a temperature element is not similarly increased when accompanied by taste. In addition, a within-compound association formed between odor and the partner component appears to be an important mechanism underlying the potentiation effect. This was demonstrated by a related decrease in the odor aversion following a decrease in the aversion to the stimulus compounded with odor. If we assume that the simultaneous conditioning of stimuli establishes a within-compound association between them as proposed by Rescorla & Cunningham (1978), then it seems plausible that there are varying levels of strength of those associations. Odor potentiation may be due to the presence of a strong association between odor and taste or odor and temperature such that test presentations of odor activate the taste-US or temperature-US association as well as the odor-US association. The absence of temperature potentiation may be because the association between taste and temperature may not be of sufficient strength to activate the taste-US association. If so, one possible means of increasing the probability that other CS-US associations are activated when temperature is conditioned and subsequently presented might be to condition temperature with both odor and taste

simultaneously. The presence of more components means potentially more within-compound associations, which in turn may summate to enable temperature to activate the odor-US and taste-US associations to cause temperature potentiation.

The purpose of the following experiment was to determine whether a temperature potentiation effect can be produced by increasing the number of components simultaneously conditioned with it, thereby increasing the number of associations with the US. To do this, rats received conditioning to a three-component compound consisting of odor taste and temperature stimuli. Following conditioning to the compound, one of the elements was conditioned. Consumption levels during test presentations of each separate stimulus were then compared. To the degree that learning about temperature is enhanced by within-compound association learning, the temperature presented in compound should be rejected more than the temperature presented alone. The design of this experiment also permitted the determination of whether a potentiation effect is established for taste when conditioned with odor and temperature, or to odor when conditioned with taste and temperature.

Method

Subjects. The subjects were 24 Holtzman male rats approximately 90 days old at the start of the experiment. All animals were housed in individual hanging wire-mesh

cages.

Apparatus. The apparatus was identical to that used in previous experiments. The odor (ALM and PINE) and temperature (HOT and COLD) cues were identical to those used in previous experiments. The taste cues were sucrose (SUC) as in previous experiments and a 2% (w/v) solution of sodium chloride (SALT). The three-component compound was created by heating or cooling the taste solution to one of the temperature levels and putting 1 ml of the odor solution on the filter paper in the experimental chamber.

Procedure. All animals were adapted to a water deprivation schedule that permitted access to room-temperature distilled water for a period of 15 min each day. During adaptation and throughout the experiment, food was removed just prior to fluid access and returned approximately 1 hr later. For a 5-day period, all animals were habituated to drinking for 5 min in the conditioning chamber located in a separate room. Distilled water at room temperature was given approximately 1 hr later in their home cages.

Table 2 (see Appendix 1) presents an outline of the stimulus conditioning and testing sequence of the experiment. Animals were divided into three groups of eight animals each. A slightly different labelling notation was required for this experiment. All animals were given an A,BXY conditioning treatment where A and B were different stimuli of the same modality and X and Y were stimuli of

different modalities. Each member of each group received exposure to one of the eight possible combinations of odor, taste, and temperature stimuli. For Group O, A and B were ALM and PINE, X was either SUC or SALT, and Y was either HOT or COLD. For Group Ta, A and B were SUC and SALT, X was either HOT or COLD, and Y was either ALM or PINE. For Group Te, A and B were HOT and COLD, X was either ALM or PINE, and Y was either SUC or SALT.

On Day 1, each animal received a 5-min exposure to BXY. On Day 3, all animals received a similar exposure to A. Immediately following exposure to the experimental solutions, each animal was given a 5 ml/kg ip injection of .6 M LiCl and returned to its home cage. Days 2 and 4 were recovery days during which all animals were given a 5-min access to distilled water in the conditioning chambers.

Testing was conducted on Days 5 and 6. On Day 5 half the animals in each group were given access to A and half were given access to B. On Day 6 each received the other stimulus.

Results

Training data. During the conditioning periods, mean consumption of the experimental stimuli collapsed over two days fell within a range from 7.8 gm for SALT to 9.6 gm for HOT. The differences in consumption of each stimulus were not significant, $Fs<2.0$, $ps>.10$. Average consumption (collapsed across experimental solutions) on the first and

second conditioning days were 7.4 gm and 7.9 gm, respectively, indicating that poisoning on the first conditioning day did not interfere with consumption on the second conditioning day.

Test data. During testing, animals were given separate exposures to either ALM and PINE, SUC and SALT, or HOT and COLD. Figure 5 (see Appendix 2) shows a comparison of the average consumption during the presentation of each stimulus over the two days of testing, separated according to whether each was A or B. The data were analyzed using ANOVA with one between-subjects factor, modality (odor vs. taste vs. temperature), and one within-subjects factor, treatment (A vs. B). A reliable main effect of treatment, $F(1,21)=8.90$, $p<.001$, indicated that animals consumed more during exposure to B than A, thus demonstrating a potentiation effect. The main effect of modality was significant, $F(2,21)= 45.95$, $p<.001$. The Modality x Treatment interaction was significant, $F(2,21)=4.13$, $p<.05$. Individual comparisons showed that consumption during exposure to the odor stimuli was significantly less during B than A, $t(7)=4.35$, $p<.01$. There was no significant difference in consumption during A and B as taste cues, $t(7)=0.49$, $p>.05$, nor between A and B as temperature cues, $t(7)=1.09$, $p>.05$. Comparing A test consumption across taste, odor, and temperature groups indicated significantly less intake occurred during presentation of the taste alone than the odor alone, $t(14)=5.37$, $p<.01$. In addition, animals

consumed less of the taste alone than the temperature alone, $t(14)=6.85$, $p<.01$. The difference between amount consumed during exposure to odor alone and temperature alone was not significant, $t(14)=1.71$, $p>.05$. Comparisons of B test consumption across these same groups revealed differences between all groups. Consumption during odor exposure was less than consumption of both temperature, $t(14)=4.89$, $p<.01$ and taste, $t(14)=2.60$, $p<.01$, while the amount consumed during exposure to the temperature was less than consumption of taste, $t(14)=6.76$, $p<.01$.

Discussion

The results of this experiment indicated that an aversion conditioned to a novel temperature stimulus is not potentiated by the presence of more than one other stimulus during conditioning. Animals drank equivalent amounts of the temperature conditioned in compound and the temperature conditioned separately. Apparently, then, the presence of more components during conditioning does not necessarily result in the summation of the associations between temperature and the accompanying components. The absence of temperature potentation remains inconsistent with a within-compound association account.

The present findings also indicated that the aversion to an odor when conditioned in a three-component compound can be enhanced similar to the odor potentiation effect observed when conditioning two components. Animals showed a

stronger aversion to the odor conditioned with both taste and temperature in compound than to the odor conditioned alone. Therefore, the parameters of odor potentiation can be extended to reinforced compounds containing more than two components.

The present experiment also examined the effect of conditioning taste in compound upon the development of a taste aversion. The results indicated that learning about taste is not potentiated by the presence of odor and temperature during conditioning. The aversions demonstrated to the taste stimuli were large regardless of whether the particular taste had been conditioned in compound or alone. These findings are consistent with other reports that indicate no significant effect on the conditioning of the taste cue following odor-taste conditioning (Palmerino et al., 1980; Rusiniak et al., 1979) and color-taste conditioning (Clark et al., 1979; Lett, 1980).

However, some investigators (Westbrook, Homewood, Horn, & Clarke, 1983) have reported an attenuation of the taste aversion following simultaneous conditioning with odor. While such findings appear consistent with many models of conditioning which assume compounded stimuli compete with one another for associative strength (Mackintosh, 1975; Rescorla & Wagner, 1972), there were features of the procedures that may have contributed to obtaining an apparent taste attenuation effect. In a typical experiment (e.g., Bouton & Whiting, 1982) that demonstrated taste

attenuation, one group of animals was conditioned to a taste cue alone and a second group was reinforced following taste in compound with odor. During subsequent testing, the taste was considerably less aversive to animals conditioned with the odor-taste compound. Because the overall exposure to odor was not the same for both groups of animals, it is unclear whether the relatively weak taste aversion was due to the presence of odor or resulted from generalization decrement between conditioning (when the odor and taste were presented together) and testing (when the taste was presented alone). In the present experiment, two tastes were compared against each other within each animal during the test for potentiation. Such an arrangement seems better able to detect evidence of potentiation due to the presence of another cue during conditioning.

VI. General Discussion

The present demonstration of potentiation replicates previous investigations by Durlach and Rescorla (1980) and Rusiniak et al. (1979) of enhanced odor conditioning following aversive compound conditioning with taste. The results parallel the potentiation of color cues accompanied by taste (Brett et al., 1976; Clark et al., 1979; Galef & Osborne, 1978; Lett, 1980). The present experiments also indicate that the odor potentiation effect can be produced when the stimulus accompanying odor is temperature (Experiment 2). However, presenting temperature or taste in compound with each other (Experiment 3) or together with odor (Experiment 4) does not similarly potentiate the development of aversions to either taste or temperature.

These experiments also sought to determine the mechanism underlying the potentiation effect. Two hypotheses about this structure were distinguished: the memorial indexing hypothesis (Garcia & Rusiniak, 1980) and the within-compound association hypothesis (Durlach & Rescorla, 1980). The memorial indexing account assumes that potentiation reflects a stronger odor-US association, whereas the within-compound association account postulates the formation of an association between the elements of the compound that allows the taste-US association to add to the odor-US association. Consistent with the within-compound hypothesis, the present results indicated that extinguishing the taste or temperature aversion following conditioning

caused a decrement in the response to the odor. Moreover, these experiments revealed an extinction effect even when no preconditioning exposure to the compound stimuli was given; this is contrary to the suggestion by Lett (1983) that the within-compound association evidenced by Durlach and Rescorla (1980) had been formed during the pre-exposure to the compound stimuli.

However, a general theory of within-compound learning as the basis of potentiation cannot be universally applied to all classes of stimuli in all situations. The problem for this account is to explain the enhancement of odor, but not taste or temperature, aversion learning during compound conditioning. In addition, while potentation has not been reported using non-food-related stimuli, the account presently offers no requirements that the CSs and the US be specific to food regulation. Finally, and perhaps more importantly, the within-compound account does not specify a priori when stimuli in compound result in overshadowing or potentiation.

One possible way to reconcile a stimulus-specific potentiation effect into the within-compound association account can be derived from a general description of conditioning in terms of bidirectional connections. The bidirectional conditioning hypothesis (Asratyan, 1967; Pavlov, 1927; Razran, 1971) assumes that the traditional stimulus pairings activate discrete cortical areas corresponding to each of those stimuli and two separate,

directional connections are formed between the two cortical areas. With regard to compound conditioning situations, this assumption implies that a CS1-CS2 presentation results in one association governing the activation of CS2 by CS1, and one governing the activation of CS1 by CS2.

The results of the present experiments seem consistent with a view of two independent associations if the connections are assumed to vary depending upon certain features of the components. One distinguishing feature of CSs susceptible to potentiation (odor and color) is that they can be perceived at a distance from their source. In contrast, components that have been paired (taste and temperature) with these distal stimuli and do not develop enhanced CRs can be characterized as proximal stimuli. The nature of a distal-proximal compound CS means that, for example, a rat would be able to smell an odor-taste compound at least a few seconds before it tastes it. Hence, such compounds may be regarded as serial compounds rather than simultaneous compounds. In the present experiments, the serial sequence would be odor-taste-illness or odor-temperature-illness. Presumably, a forward within-compound association would be established between odor and taste or between odor and temperature, and a backward within-compound association would be established between taste and odor or between temperature and odor. If, as is generally held, forward associations are stronger than backward associations, odor would be potentiated more

readily than taste or temperature. That is, the associations activated during testing by odor (e.g., odor-illness, odor-taste, and in turn, taste-illness) are all forward associations. In contrast, test presentations of taste would activate a forward taste-illness association and a backward taste-odor association, which may not be strong enough to activate the odor-illness association. Summation of the taste-illness and odor-illness associations could not occur to produce an enhanced taste aversion. Thus, potentiation may simply represent a case of serial compound conditioning in which the within-compound associations are asymmetrical in strength.

In addition, the formation of within-compound associations, and therefore potentiation, is likely under the conditions of the present experiments because the odor is paired with a taste and/or temperature which is neutral. Holland (1985) has found that, during serial S1-S2 conditioning, a neutral S2 facilitates the formation of an stimulus-stimulus (S-S) within-compound association. The results following the extinction phase in Experiment 2 also suggest the formation of S-S within-compound learning.

The modified within-compound association account, developed above, implies that potentiation is a product of a general associative mechanism (within-compound learning) among compounded elements, but that the operation of this mechanism has certain stimulus-specific effects. The involvement of both general and specific features in a

learning theory is not inconsistent with a growing pattern in the study of animal learning within the past decade. Traditional approaches to learning are being challenged to account for observations of learning phenomena that are contrary to general laws of associative learning and appear to illustrate biologically specialized mechanisms (e.g., Bolles, 1970; Rozin & Kalat, 1971; Seligman, 1970; Shettleworth, 1972). Many investigators have proposed modifications of, or additions to, general process learning theory (e.g., Domjan & Wilson, 1972; Krane & Wagner, 1975; Revusky, 1977). New principles such as belongingness (e.g., Revusky, 1971) and stimulus similarity (Rescorla & Furrow, 1977) have been suggested to account for differences in the rate of association formation between certain combinations of CSs and USs. Occurrences of potentiation may warrant the introduction of a "distal-proximal" principle that deals with certain combinations of elements within a compound CS.

Overall the present data suggest that potentiation is a robust phenomenon that can occur in compound conditioning preparations involving food-related stimuli. Quite apart from their commentary on food-aversion learning, these results have several implications for our understanding of Pavlovian conditioning in general. First, they indicate that organisms can learn about more than one stimulus at a time without detriment to learning about the others (e.g., overshadowing, blocking). Second, attending to within-compound learning allows for the possibility that

Pavlovian conditioning may be facilitated, rather than overshadowed, at least when certain CSs are combined.

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Appendix 1

TABLE 1

Design of Experiment 2

GROUP	CONDITIONING	EXTINCTION	TEST
TaExt	A+ BX+	X-	A B
TaNo	A+ BX+	H2O	A B
TeExt	A+ BX+	X-	A B
TeNo	A+ BX+	H2O	A B

Note: A, B - almond or pineapple odors

X - taste or temperature

\+ - LiCl US

\- - no US

Each group received conditioned presentations of an odor alone (A) and a second odor (B) in compound with either taste or temperature (X). Two of the groups then received extinction trials involving the X component, while the remaining groups were given exposure to distilled water.

TABLE 2

Design of Experiment 4

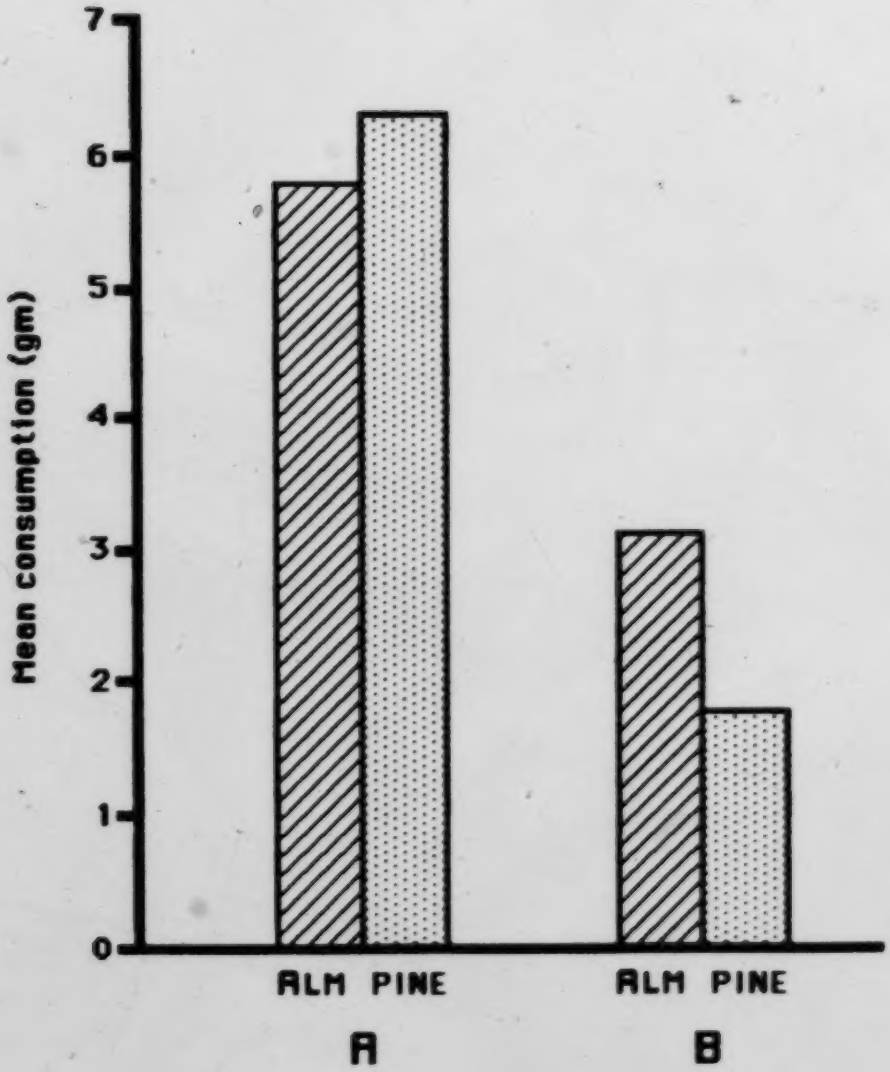
STIMULUS COMBINATIONS		CONDITIONING Day 1	CONDITIONING Day 3	TEST Day 5-6
SucAlmHot				
SucPineHot	Group O	BXY	A	A B
SaltAlmHot			(ALM/PINE)	
SaltPineHot				
SucAlmCold	Group Ta	BXY	A	A B
SucPineCold			(SUC/SALT)	
SaltAlmCold				
SaltPineCold	Group Te	BXY	A	A B
			(HOT/COLD)	

Note: SUC - sucrose; SALT - sodium chloride
ALM - almond; PINE - pineapple
HOT - 40°C; COLD - 10°C
A - stimulus conditioned alone
B - stimulus conditioned in compound
X and Y - remaining stimulus modalities.

Each group received conditioned presentations of stimuli involving odor, temperature, or taste alone (A) and a second stimulus of the same modality (B) in compound with both of the remaining modality stimuli (X and Y), such that all possible stimulus combinations were presented within each group.

Appendix 2

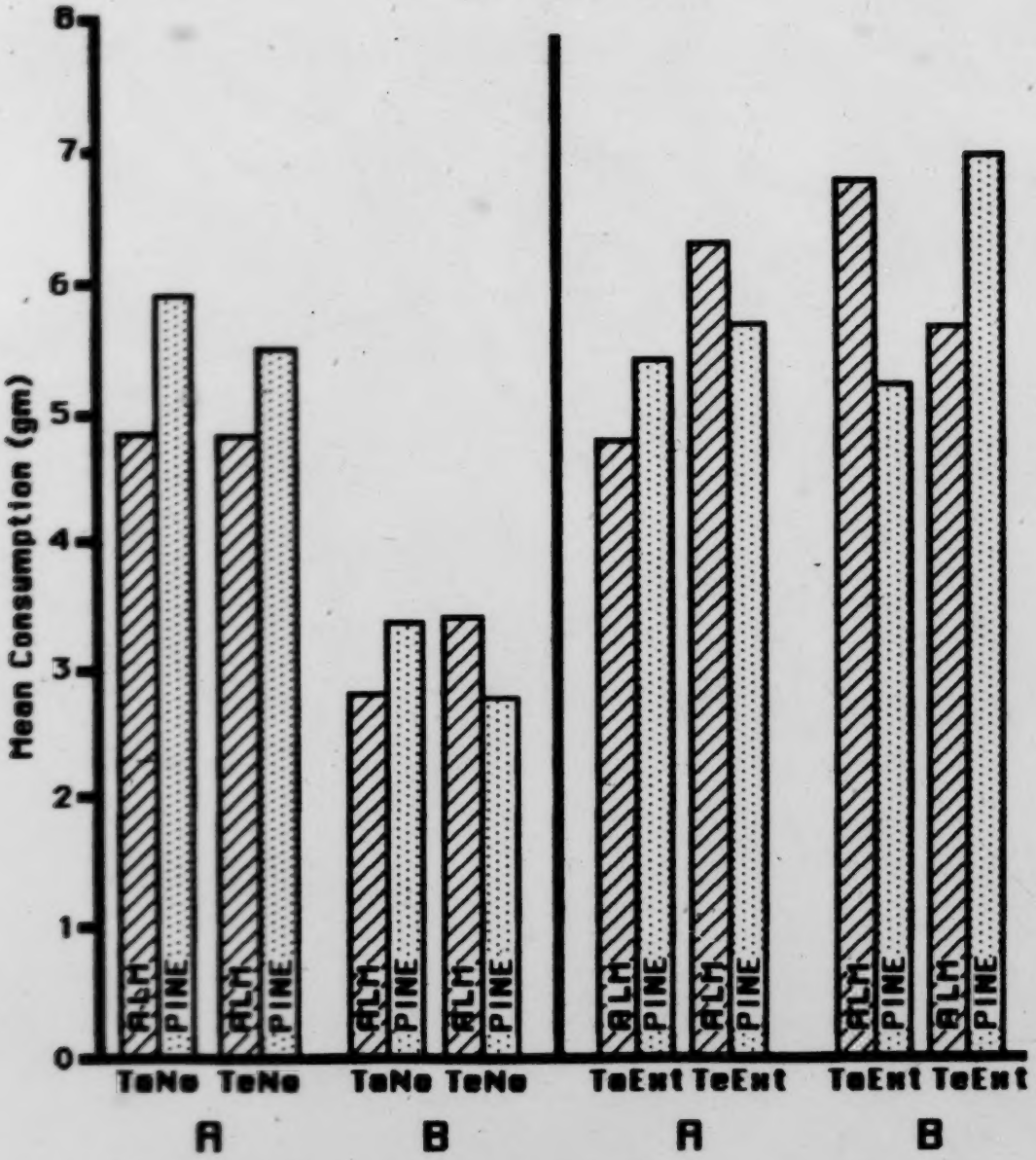
Figure 1
Results of Experiment 1



Note: Mean consumption of distilled water during exposure to almond (ALM) and pineapple (PINE) over the two test days. Each animal received conditioning to one odor alone (A) and one odor (B) in compound with taste.

Figure 2

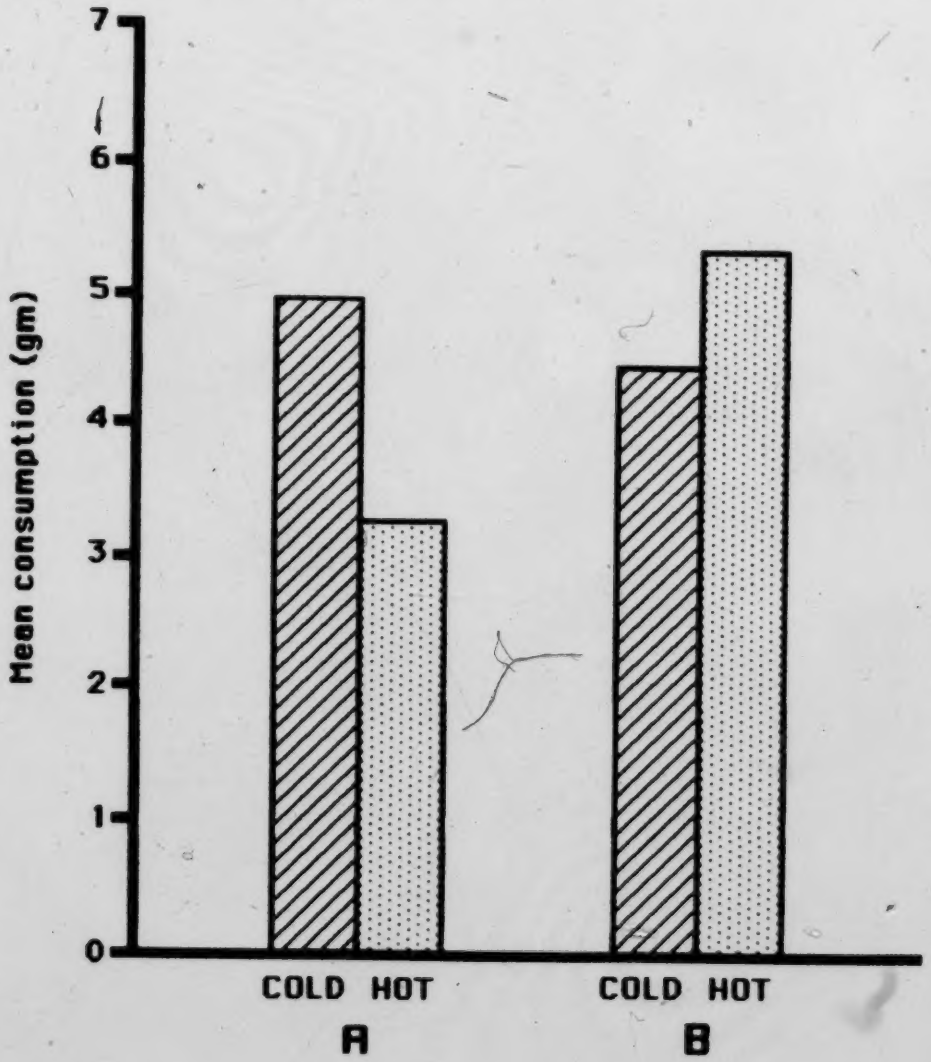
Results of Experiment 2



Note: Mean consumption of distilled water during exposure to almond (ALM) and pineapple (PINE) odors during test days. Each animal received conditioning to one odor alone (A) and one odor (B) in compound with teste (Te) or temperature (Te). Half the animals were then given extinction trials involving either Te (Group TeExt) or Te (Group TeExt). The remaining half were given no extinction training (Groups TeNo and TeNo).

Figure 3

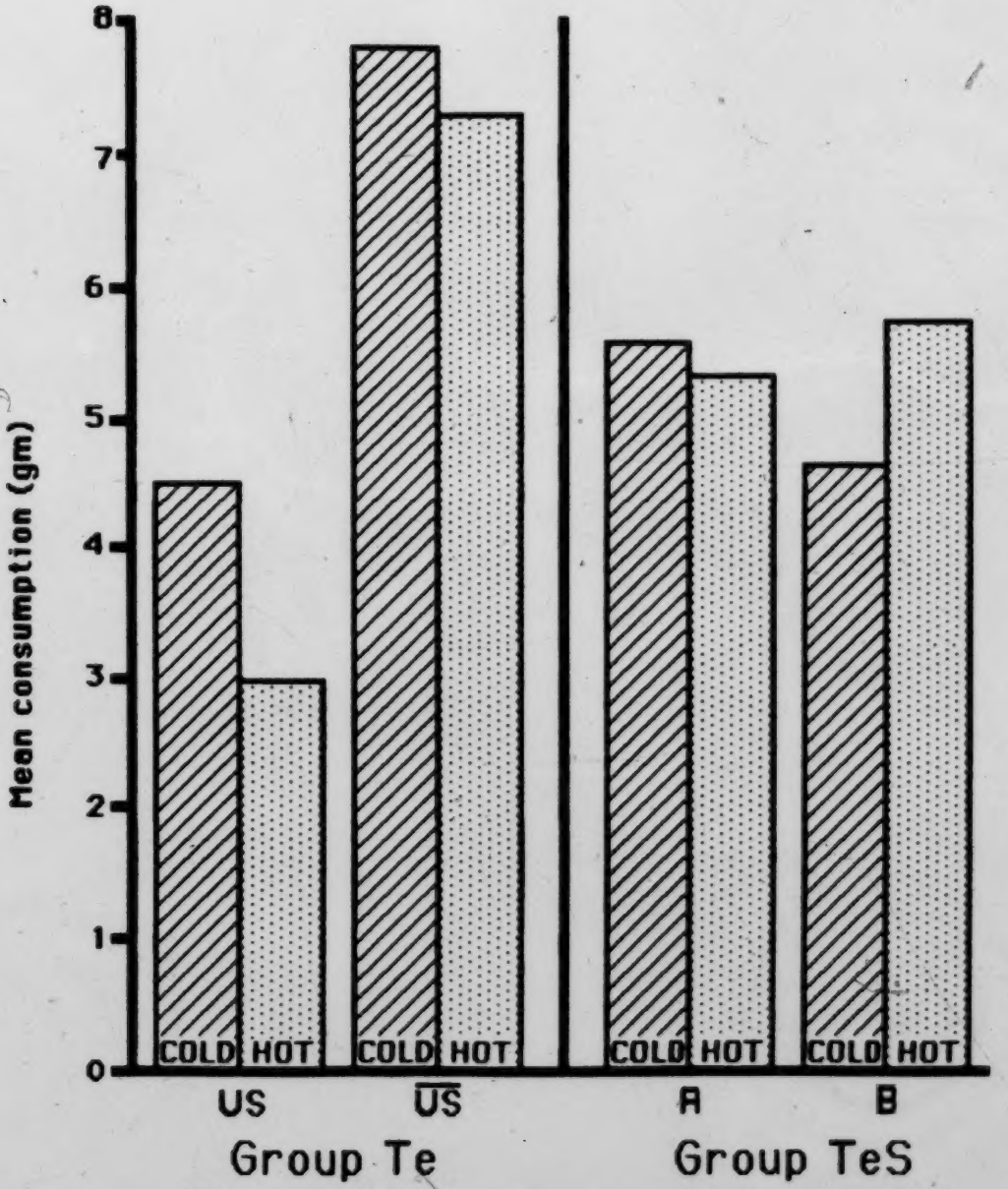
Results of Experiment 3A



Note: Mean consumption of distilled water heated (HOT) or cooled (COLD) during test days. Each animal received conditioning to one temperature cue alone (A) and one temperature cue (B) with taste.

Figure 4

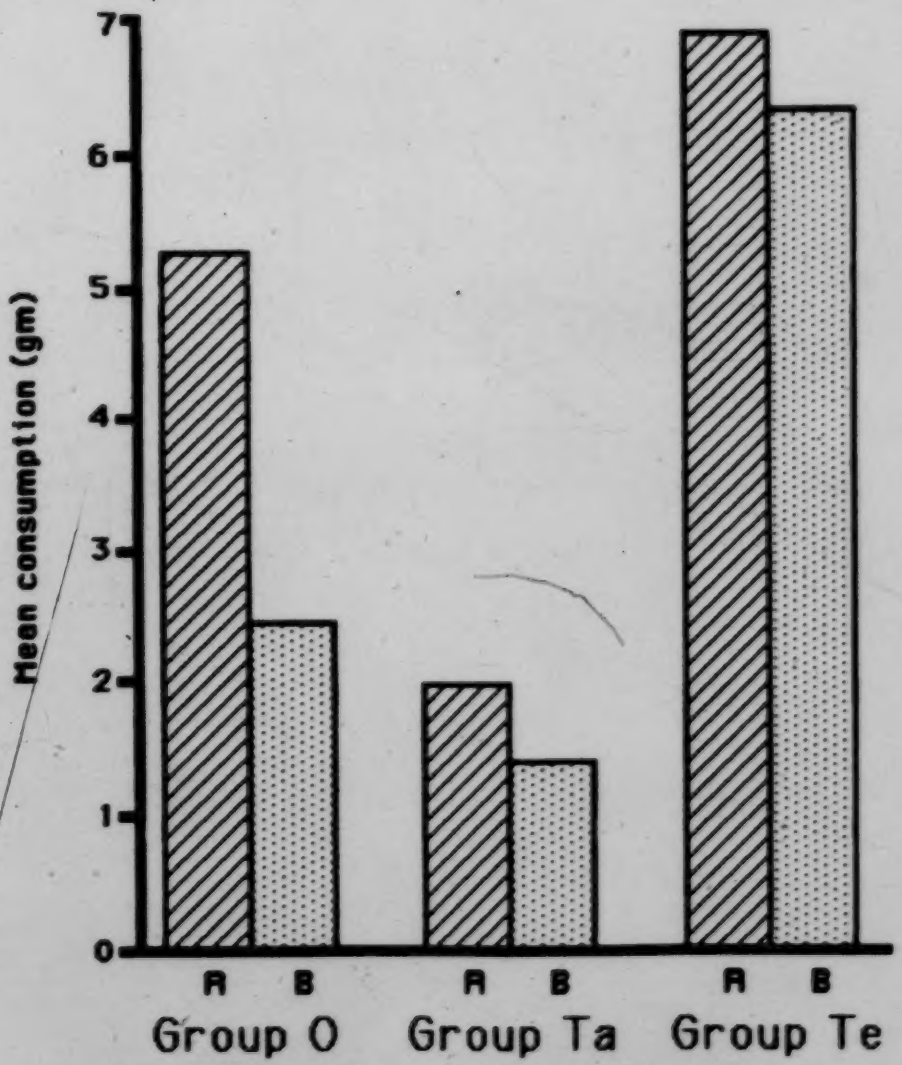
Results of Experiment 3B



Note: Mean consumption of distilled water heated (HOT) or cooled (COLD) during test days. Group Te received conditioning (US) to one temperature cue and no conditioning ($\overline{US}$) to the other. Group TeS received conditioning to one temperature alone (A) and one temperature (B) in compound with taste.

Figure 5

Results of Experiment 4



Note: Mean consumption of distilled water during exposure to the target stimuli during test days. Each animal received conditioning to one target stimulus alone (A) and one target stimulus in compound (B) with two stimuli of two different modalities. For Group O, the target stimuli were odors; for Group Te, the target stimuli were tastes; and for Group Te, the target stimuli were temperatures.